Mathematical description of heat transfer in living tissue (Part II)

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Part I

Appendix

Chapter 1

Possible cooperative mechanisms of self-regulation in large natural hierarchical systems

In the previous Chapters we considered in detail the mathematical model for the vascular network response to variations in the tissue temperature. We have found that the distribution of the blood temperature over the venous bed aggregating the information of the cellular tissue state allows the living tissue to function properly. We think that this property is one of the general basic characteristics of various natural hierarchical systems. These systems differ from each other by the specific realization of such a synergetic mechanism only. In the present Chapter generalizing the results obtained above we consider typical examples of hierarchical systems which can be met in ecology, economy, etc.

1.1 What the cooperative self-regulation is from the general point of view

Large hierarchical systems occurring in nature are characterized by such a great information the flow that none of their elements can possess whole information required of governing the system. Here we want to focus attention on the fact that in such large hierarchical systems there can be a cooperative mechanism of regulation which involves an individual response of each element to the corresponding hierarchical piece of information and leads to the ideal system functioning due to self-processing of information.

As a evident example of such systems we may regard living tissue where blood supplies the cellular tissue with oxygen, nutritious products, etc. and

at the same time withdraws CO_2, products resulting from living activities of the cellular tissue. A similar situation takes place in respiratory systems where oxygen reaches small vessels (capillaries) going through the hierarchical system of bronchial tubes.

The organization structure of large firms is a clear example of economic hierarchical systems. Managers of all functions and all levels make up a management network [85]. Roughly speaking, the management network controls the money flow towards the organization bottom comprising workers as well as the flow of products in the opposite direction. In performing technological processes wages paid to workers actually transforms into the firm products.

The existence of a tremendous amount of goods in market, in contrast to a relatively small number of raw materials shows that there must be large hierarchical systems in the market structure. So, it is possible to single out certain drafts of hierarchical systems inside a given branch of industry. In this context we note that goods flow on such structures and after reaching the consumers transform into money flow in the opposite direction.

Concerning ecological systems we would like to note that they are also complex in structure, can involve a larger number of "predator-pray" levels and are grounded on some basic medium (for example, plankton) [79, 33, 37]. Dynamics of ecosystems is governed by a biomass and energy flow on trophic networks.

In the present Chapter we, first, extend the thermoregulation model stated above in order to show that the cooperative self–regulation mechanism is actually based only on the general conservation laws in systems whose evolution is governed by the minimum conditions for energy dissipation [60, 61, 62]. Let us recall once more the main characteristics that the system under consideration should possess. Such a system is grounded on a certain distributed basic medium. This medium is a living continuum which for its activities needs nutrition or living and a draining system that withdraws products resulting from its living activities. For this purpose there is a complex transport network through which transport agent supplies and drains the basic medium. The architectonics of the transport network should be organized in such a manner that a flow of a transport agent through the living medium be the same at each point, all other factors being equal. To meet this condition the transport network may involve supplying and draining bed of the tree form. In principle, the two beds can coincide with each other in real space. Interaction between the transport agent and the basic medium causes interchange of the supplied and withdrawn products. The transport agent flow through the basic medium should keep up the concentrations of these products inside a certain region called the vital region, which is the aim of regulation.

Due to the transport agent motion being accompanied by energy dissipation it is necessary that a certain external force to be applied to the system that affects the overall flow of the transport agent. In living tissue the blood pressure plays the role of this external force. In order to analyse behavior of ecological systems it is possible to apply the general principles of nonequilibrium thermodynamics [78]. In economic systems the total utility function [89] seems to play the role of the external force causing products and a money flow.

In contrast to artificial systems, natural ones are able to adapt to variations in the environment. Under ordinary conditions the behavior of natural system as a whole and the individual behavior of its different elements are likely to follow the strategy of the minimum expenditure rate. They agree with the minimum entropy production principle stated in nonequilibrium thermodynamics [78]. However, for such complex and nonequilibrium systems as biological and ecological ones, specification of particular expressions for the entropy production rate is far from being solved and the minimum entropy production principle can be applied to these systems at the phenomenology level only.

It should be noted that, broadly speaking, in systems where functionals similar to entropy production play the governing role transport agent flow is actually a free variable. In other words the transport agent flow distribution over the living system is directly governed by a certain potential and each element of the system can control solely its own state rather than transport agent flow through it and other elements. So, it is likely that in large hierarchical natural systems none of their elements cannot only possess the total information on the system but also directly determine transport flow through the network. In these systems there should be a certain cooperative mechanism of adaptation based on the individual element control over its own state. The aforesaid allows us to imagine a living system as one involving two characteristic parts. The former is living media that consume the products needed for their activity. The second is a hierarchically organized network flow through which transport agent delivers these products to each point of the living medium. The living medium is made up of a large number of elements similar in the specific function, therefore it may be treated as a continuum. The supplying network is embedded into this continuum and in its turn involves two parts. One of them supplies the living medium with the products needed for life activities and the second withdraws products of life activities from the living medium. Because the transport agent flow with the life activity products in the draining bed leaves the living medium and is directed from higher to lower hierarchy levels it automatically contains all information of the living medium state distributed over the draining bed. If this information is transmitted to the supplying bed in such a manner that each its element responds to the corresponding piece of information then, the supplying bed as a whole will be able to respond properly to the living medium demand. Feasibility of synergetic self-regulation in hierarchically living systems based on such information transmissions and the corresponding response of the supplying bed is the subject of the present paper.

A real living system should contain a certain element or a subsystem that, first, causes the cyclic transport agent motion inside the living system, second, provides the required composition of the products for life activity in the transport agent flow at the supplying bed entry. The properties and functioning details of this element or subsystem are beyond the self-regulation problem. Therefore, in the present model it will be described as a certain element that joins the stems of the supplying and draining bed and is characterized by a force causing the transport agent motion as a whole.

Mathematical model and theory of large hierarchical systems under consid-

eration and different aspects of the problem of information processing have been considered in [60, 61, 62]. It should be noted that the problem of processing a huge amount of information is also met in constructing and optimizing large artificial systems similar to transport networks [13, 41]. Their elements also do not possess the whole information, however, as a rule, their local interaction with the nearest neighbors (in space or hierarchy) can directly control the corresponding mass flow going through them [13, 41]. Elements of the natural systems either do not possess the whole information or has no capability for controlling the local flows. They are able to vary their individual characteristics only, which through the cooperative interaction of all hierarchy levels leads to the redistribution of a mass flow over the supplying bed in the proper way.

1.2 Generalized mathematical model of living system

Let us consider a system consisting of the distributed living medium $\mathcal{M}$ and the transport hierarchical network $\mathcal{N}$ (Fig. 1.1). The transport network involves supplying and draining beds of the tree form shown in Fig. 1.1. by the left and right - hand side networks and an external element S joining the tree stems. The transport agent flowing through the former bed supplies the living medium $\mathcal{M}$ with the products needed for life activities. At the same time transport agent withdraws products of living activities from the living medium through the draining bed. The medium $\mathcal{M}$ is considered to be a d - dimensional homogeneous continuum. For any integer number n the medium $\mathcal{M}$ can be represented as the union $\mathcal{M} = \cup\mathcal{M}_n$ of 2^{nd} similar disjoint domains $\mathcal{M}_n$ whose characteristic size is $l_0 2^{-n}$ where l_0 is the mean size of the medium $\mathcal{M}$ as a whole. The domains $\{\mathcal{M}_n\}$ will be called fundamental domains of level n and those of the last level N will be also referred as elementary domains. All the fundamental domains of a given level form the basic medium $\mathcal{M}$.

Geometry of both the beds is assumed to be the same, so, we specify it for the supplying bed only. The stem of this bed splits into $g = 2^d$ branches of the first level (Fig. 1.1). Each of the first level branches, in turn, splits into g branches of the second level and so on. The branches of the last level (N) are directly connected with living medium $\mathcal{M}$. The bed is organized in such way that each branch i of a given level n supplies a certain domain $\mathcal{M}_n^i$ as a whole. Each elementary domain is bound up with the one of last level branches. The last level number N is assumed to be much larger than unity: $N \gg 1$, and the length l_N may be regarded as an infinitely small spatial scale.

For the sake of simplicity we assume that the living medium domain $\mathcal{M}$ is a d-dimensional cube of edge l_0 and, corespondent, a fundamental domain of level n is a cube of edge $l_0 2^{-n}$. Fragments of the supplying bed architectonics embedded into the living medium for $d = 2$ and $d = 3$ is shown in Fig. 1.2,1.3. The transport agent flow is directed from lower to higher levels of the supplying bed and in the opposite direction on the draining bed.

Figure 1.1: The stucture of hierarchical system.

In accordances with network architectonics (Fig. 1.2,1.3) the host transport agent flow goes into and out of the cube $\mathcal{M}_0$ through one of its corners. The host transport agent flow of the supplying bed reaches the cube center O_0 where it branches out into 2^d flows of the first level. Each transport agent flows of the first level reaches a center O_1 of one of the 2^d cubes (called the fundamental domains of the first level) that compose together the cube $\mathcal{M}_0$. At the centers $\{O_1\}$ each of the first level transport agent flows in its turn branches out into 2^d second level flows. Then, the flow branching is continued in a similar way up to level $N \gg 1$.

Transport agent flow going through branches of any level except for the last level does not interact with the living continuum $\mathcal{M}$. When the transport agent flow reaches one of the last level branches of the supplying bed, for example branch i, it uniformly penetrating through the elementary domain $\mathcal{M}_N^i$ containing the branch i delivers the products needed for life activities at each point of the domain $\mathcal{M}_N^i$. At the same time transport agent going through the domain $\mathcal{M}_N^i$ is saturated with the life activity products, thereby it withdraws the life activity products from the domain $\mathcal{M}_N^i$ and transports them through the draining bed out of the living system.

The state of the medium $\mathcal{M}$ will be described by a certain field θ taken to be a measure of the concentration of the life activity products, which in turn, characterizes the life activity intensity. The dynamics of the field θ in the living medium $\mathcal{M}$ is controlled by volumetric generation due to living activities, disappearance caused by draining the life medium, and diffusion of life activity products between elementary domains. Therefore, the field θ is considered to

Figure 1.2: The fragment of the transport agend flow network under consideration ($d = 2$).

Figure 1.3: The fragment of the transport agend flow network under consideration ($d = 3$).

evolve according to the equation

$$\frac{\partial \theta}{\partial t} = D\boldsymbol{\nabla}^d \theta + q - \theta\eta, \tag{1.1}$$

where D is the diffusivity, $\boldsymbol{\nabla}^d$ is the d-dimensional Laplace operator, q is the generation rate and η is the volumetric rate of the transport agent flow. Since, branch i of the last level supplies the elementary domain $\mathcal{M}_N^i$ of the living medium as a whole; the current J_i of the transport agent in branch i and the transport agent flow rate η in the corresponding domain are related by the expression

$$J_i = \int\limits_{\mathcal{M}_N^i} d\mathbf{r}\eta. \tag{1.2}$$

The last term in equation (1.1) implies that due to interaction between the living medium and transport agent in the last level branches the concentrations of life activity products $\mathcal{M}$ inside a living medium elementary domain $\mathcal{M}_N^i$ and in the transport agent going through the corresponding last level branch i of the draining bed became equal to each other. Therefore, first, transport agent going through the draining bed can be also characterized by variable θ and the value θ_i of the variable θ corresponding to branch i and can be different for various branches due to possible nonuniformities in life activity of a living medium. Second, the value θ corresponding to branch i of the last level and distribution of the field θ over the elementary domain $\mathcal{M}_N^i$ must be related as

$$J_i\theta_i = \int\limits_{\mathcal{M}_N^i} d\mathbf{r}\theta\eta. \tag{1.3}$$

The pattern of the transport agent current flow $\{J_i\}$ on the network $\mathcal{N}$ obeys the conservation law at branching points. So, for a given branching point B we can write

$$\sum_B J_{\text{out}} = J_{in} \qquad \text{or} \qquad \sum_B J_{in} = J_{\text{out}}, \tag{1.4}$$

where J_{in} and J_{out} are the transport agent currents on branches going in and out of the point B and the sum runs over all the branches leading to or out this point. The former and latter expressions are corresponding to the supplying and draining bed, respectively. The life activity products moves with transport agent flow through the draining bed, thus the value $J_i\theta_i$ can be regarded as the current of the variable θ_i on branch i. As the transport agent going through the draining bed towards its stem does not interact with the living medium, the pattern $\{J_i\theta_i\}$ should also obey the conservation law at the branching points of the draining bed. The latter allows to write for a given branching point B of the draining bed

$$\sum_B (J_i\theta_i)_{in} = (J_i\theta_i)_{\text{out}}. \tag{1.5}$$

Equation (1.1), among with expressions (1.2) and (1.3) describe distribution of the field θ over the living medium and its relation with the transport agent flow through the transport network. Equation (1.4) and (1.5) reflect the general laws of transport phenomena in the supplying and draining beds. Now we specify the way how the system controls the transport agent flow through the network $\mathcal{N}$. First, it certain effort is needed for the living system to move transport agent through the supplying and draining beds. Therefore, it would appear reasonable that the living system tries to minimize the total energy dissipation due to transport agent motion. In mathematical terms the total energy dissipation caused by transport agent motion through the supplying and draining beds as well as through the element S is represented in the form

$$\mathcal{D}\{J_i\} = \frac{1}{2}\sum_i R_i J_i^2 - J_0 E_{ext}. \tag{1.6}$$

Here R_i is a kinetic coefficient of branch i, E_{ext} is the force that gives rise to transport agent motion through the network $\mathcal{N}$ as a whole, J_0 is the transport agent flow through the tree stems and the sum runs over all the branches of the supplying and draining beds. Therefore the flow pattern on the supplying and draining beds as well as the coefficient collection $\{R_i\}$ must be mirror images of each other within the reverse flow direction.

Keeping in mind that the system tries to minimize the energy dissipation due to transport agent motion we postulate that the distribution $\{J_i\}$ of transport agent flow over the network $\mathcal{N}$ corresponds to the minimum of the functional $\mathcal{D}\{J_i\}$ subject to conditions (1.4). As has been mentioned in Section 1.1 the distribution $\{\theta_i\}$ can be treated as the aggregated information on the living medium state. In particular, the variable θ_i corresponding to branch i describes the state of the corresponding fundamental domain $\mathcal{M}_n^i$ as a whole. Therefore, in order to complete the given model we should specify the response of the transport network $\mathcal{N}$ to variations in the variables $\{\theta_i\}$. Due to supplying and draining beds being mirror images of each other we may describe this response for the draining bed only. We assume that for each branch, for example the branch i, time variations in the transport coefficient R_i are directly controlled by the variable θ_i assigned to this branch.

When time variations of the distribution $\{\theta_i\}$ are quasistationary the coefficient R_i corresponding to branch i of level n is the explicit function of the variable θ_i, i.e. $R_i = R_n(\theta_i)$. The general properties of the $R_n(\theta_i)$ dependence are actually determined by the Fact that the transport agent flow through the network $\mathcal{N}$ should grow with increase in the life activity intensity. Indeed, let during the living system adapting to changes in the environment life activities of the living medium grow in intensity. The latter leads immediately to increase in the concentration of the life activity products inside the living medium, and, thus, to increase in the field θ, causing increase in variables θ_i. The higher life activity intensity, the greater amount of the products needed for life activities. Therefore, under such conditions transport agent flow through the network $\mathcal{N}$ must increase too. In other words, increase in the variable θ_i should give rise to increase of transport agent flow. As it will be shown below the coefficient R_i can be treated as a resistance of branch i to the transport agent flow through it. Thus, the function $R_n(\theta_i)$ must be decreasing with respect to the variable θ_i. Taking the aforesaid into account we represent the $R_n(\theta_i)$ dependence in terms of

$$R_n(\theta_i) = R_n^0 \phi(\theta_i), \tag{1.7}$$

where R_n^0 is a constant equal to $R_n(\theta_i)$ for $\theta_i = 0$ whose value is assumed to be the same for all the branches of one level and $\phi(\theta_i)$ is a certain universal function. The characteristic form of the $\phi(\theta_i)$ dependence is shown in Fig. 1.4a., where value θ_c matches the maximum allowable concentration of the life activity products in the living medium. When the concentration of life activity products exceeds the allowable value, that is $\theta > \theta_c$ the living medium goes beyond the vital interval and loses the capability for adapting. So, for $\theta_i > \theta_c$ the function $\phi(\theta_i)$ has to be practically constant.

Figure 1.4: Behaviour of the function $\phi(x)$ - a and the function $f(x)$ - b.

For the transport network $\mathcal{N}$ to be able to respond properly to local variations in life activities of the living medium distribution of the transport agent flow over the network $\mathcal{N}$ it should be controlled by branches of all the levels. This condition, as it will be seen below, allows us to represent the dependence of the value R_n^0 on the level number n in the form

$$R_n^0 = R_0 2^{dn} \rho(n), \tag{1.8}$$

where R_0 is a constant equal to $R_n^0|_{n=0}$ and $\rho(n)$ is a smooth function of n such that $\rho(0) = 1$ and formally $\rho(n) \to 0$ as $n \to \infty$.

Concluding description of the system response we also take into account the possible time delay of the branch response to variations in the variables $\{\theta_i\}$ and represent the evolution equation for the kinetic coefficient R_i of branch i belonging to level n as

$$\tau_n \frac{dR_i}{dt} + (R_i - R_n^0) f\left(\frac{R_i}{R_n^0}\right) = -\frac{\theta}{\theta_c} R_n^0, \tag{1.9}$$

where τ_n is the time delay of branch i response. The value τ_n is assumed to depend on the level number only. We have written the kinetic coefficient equation in such form that the term $\frac{\theta}{\theta_c}$ can be regarded a dimensionless signal which is generated by transport agent receptors of the draining bed and is sent to the corresponding branches of the supplying bed. As it follows from (1.7) and (1.9) the function $f(x)$and $\phi(x)$ are related by expression

$$[1 - \phi(x)] f[\phi(x)] = x. \tag{1.10}$$

The behavior of the function $f(x)$ is displayed in Fig. 1.4b. We introduced the function $f(x)$ related with function $\phi(x)$ only for convenience of the consideration of the linear model for branch response.

1.3 Synergetic self–regulation

In this Section we analyse the generalized model stated above. In order to study dynamics of the field θ in the living medium $\mathcal{M}$ we should know the relation

between the fields η and θ. The latter problem can be solved if we find the pattern $\{J_i\}$ of the transport agent flow on the network $\mathcal{N}$ depending on the two fields θ and η. Indeed, in this case expressions (1.2), (1.3) specifying the interaction between the living medium $\mathcal{M}$ and transport agent flow through the last level branches immediately leads us to the desired relation $\eta\{\theta\}$.

Let us find the extremal equations for functional (1.6). Following the Lagrangian multiplier method we reduce the extremum problem for functional (1.6) subject to conditions (1.4) to finding the extremal equations of the following functional

$$\mathcal{D}_L\{J_i\} = \frac{1}{2}\sum_i R_i J_i^2 - E_{ext}J_0 + \sum\nolimits_j^B P^j \left(\sum_B (J_i)_{in} - \sum_B (J_i)_{\text{out}}\right), \qquad (1.11)$$

where $\{P^j\}$ are the Lagrangian multipliers ascribed to each branching point B of the network $\mathcal{N}$, the sum $\sum_j^B$ runs over all the branching points $\{B_j\}$, and the symbols $\sum_B (J_i)_{in}, \sum_B (J_i)_{\text{out}}$ stand for the sum over all the branches going in or out of a given branching point B. (The direction of the motion on the network $\mathcal{N}$ is chosen to coincide with the transport agent flow direction.) From the conditions $\partial\mathcal{D}_L/\partial J_i = 0$ we obtain the desired extremal equations for the branches

$$J_i R_i = P^i_{in} - P_{\text{out}} \qquad (1.12)$$

and

$$P_{in} - P_{\text{out}} = E_{ext}. \qquad (1.13)$$

Here the multipliers P^i_{in} and P_{out} correspond to branching points that the given branch i goes in and out of, P_{in} and P_{out} are the multipliers ascribed to the input and output of the transport network. It should be noted that equations (1.12),(1.13) together with equation (1.4) are actually made up of the Kirchhoff equations for the network $\mathcal{N}$ where the variables $\{P^j\}$ play the role of potentials at the branching points $\{B^j\}$ causing the transport agent flow through the corresponding branches.

In this way we have reduced practically one–to–one the analysis of self-regulation problem to that considered in Chapters 11 and 12 [1] for living tissue. The latter allows us to make use of the results obtained there and to go directly to the final results for the generalized model. For the sake of simplicity we consider only the case when the supplying and draining beds respond ideally, that is when the function $\phi(\theta)$ is given by the formula

$$\phi^{\text{id}}(\theta) = \begin{cases} 1 - \theta/\theta_c & \text{if} \quad 0 < \theta < \theta_c \\ 0 & \text{if} \quad \theta > \theta_c \end{cases} .. \qquad (1.14)$$

In this case the rate of the transport agent flow will be actually determined by formula:

$$\tau\frac{\partial j}{\partial t} + j\left[1 - \beta_{cc}\frac{T - T_a}{\Delta}\right] = j_0 \ . \qquad (1.15)$$

Figure 1.5: Schematic representation of the cooperative mechanism of ideal self-regulation.

then, rewriting it we get

$$\tau\dot{\eta} + \eta\left(1 - \frac{\theta}{\theta_c}\right) = \eta_0. \tag{1.16}$$

Formula (1.16) is the desired equation governing the ideal response of the transport network to changes in living medium activities. It is of the local form, in other words, the transport agent flow rate η is determined by variations in the field θ at the same point only. Thus, the cooperative response of all the network branches is so self-consistent that the transport network delivers products needed for life only to the living medium point that "asks" the network for this. In advertent changes in delivery of products for life activity does not occur in this case, i.e. the transport network "works" ideally.

The other peculiar property of the ideal transport network is the fact that the variable θ cannot go beyond the vital interval $[0, \theta_c]$ for a long time. The latter follows from unbounded increase in the transport agent flow rate the variable η as θ tends to θ_c.

Now we discuss in detail how the ideal regulation occurs. Let us assume that, for example, in the domain Q (Fig. 1.5) the variable θ exceeds its normal value due to the balance in living activities being disturbed. In order to smother the increase in the variable θ the system should increase the transport agent flow rate η in the domain Q. The system responds by decreasing the kinetic coefficients $\{R_i\}_{\mathcal{P}}$ along the whole path $\mathcal{P}$ on the network $\mathcal{N}$ that leads from the stem of the supplying bed to the domain $\mathcal{M}$ and, then, from this domain to the draining bed stem (Fig. 1.5). Information required of this system behavior is delivered by the distribution of the variables $\{\theta_i\}_{\mathcal{P}}$ over the path $\mathcal{P}$ on the draining bed. In fact, increase of the variable θ in the domain Q must give rise to the corresponding the increase of all the variables $\{\theta_i\}_{\mathcal{P}}$. The increase in θ_i leads to decrease in the coefficient R_i. This relation between the field θ and kinetic coefficients $\{R_i\}$ of the network $\mathcal{N}$ is the essence of the self-regulation process in the active hierarchical system under consideration. Variations in the field θ located in the domain Q can, in principle, cause an alteration of the

Figure 1.6: Living medium with irregular network.

transport agent flow rate at the exterior points due to the flow redistribution over the network $\mathcal{N}$. However, in contrast to the points of the domain Q, at the exterior points, for example, at points of the domain Q' (Fig. 1.5), the decrease of different kinetic coefficients belonging to the collection $\{\Lambda_i\}_{\mathcal{P}}$ gives rise to variations in the field η different in sign. Fig. 1.5 schematically shows the sign of this effect for different branches of the path $\mathcal{P}$. In the given model due to the specific forms of function (1.16) and the right-hand side of Eq.(1.16) the net effect is reduced to zero. For other forms of these functions the second term in Eq.(1.16) will be of nonlocal form, i.e. time variations in the field η at a given point will be also determined by values of the variable θ at other points.

The way in which we got the local equation of the self–regulation could give the impression that for ideal self–regulation to be the case the transport network must be of a regular geometry with respect to branching and embedding into the space. So let us now show that the ideality of self–regulation holds for transport network of the arbitrary architectonics, at least, when the transient processes can be ignored. By way of example, we consider the transport network $\mathcal{N}$ shown in Fig. 1.6. Let at the initial time the distribution of the fields $\tilde{\theta}(\mathbf{r})$ and $\tilde{\eta}(\mathbf{r})$ over the medium $\mathcal{M}$ be predetermined. On the network $\mathcal{N}$ the patterns $\{\tilde{\theta}_i\}$, $\{\tilde{J}_i\}$ correspond to these fields. In this case by virtue of expression (1.12) we can ascribe the potentials $\{\tilde{P}^i\}$ to the branching points of the network $\mathcal{N}$. Due to the supplying and draining beds being symmetrical all the terminal points of the last level branches are characterized by the same potential P^m. First, we will show that the transport network responds to disturbances in the living medium activities in such a manner that only the transport agent flows $\{J_i\}$ vary whereas the potentials $\{\tilde{P}^i\}$ are constants. For this purpose let us consider any one branching point of the last level, e.g. the branching point B (Fig. 1.6).

Suppose that the state of the living medium $\mathcal{M}$ has changed. Assuming the potentials $\{\tilde{P}^i\}$ to be constant and taking into account (1.4), (1.5), and (1.12) we write for all the branches of this node

$$J_0 = \sum_{i=1}^{3} J_i, \tag{1.17}$$

$$J_0\theta_0 = \sum_{i=1}^{3} J_i\theta_i, \tag{1.18}$$

$$J_0 - J_0\frac{\theta_0}{\theta_c} = \frac{\tilde{P}^B - \tilde{P}^{B'}}{R_0}, \tag{1.19}$$

and for $i = 1, 2, 3$

$$J_i - J_i\frac{\theta_i}{\theta_c} = \frac{\tilde{P}^m - \tilde{P}^B}{R_i}. \tag{1.20}$$

Here $\{J_i\}$ and $\{\theta_i\}$ are the new values of the agent flows and the variable θ in the branches $i = 1, 2, 3$ and the branch 0 going into and out of the point B. The values $\theta_1, \theta_2, \theta_3$ are directly determined by the mean values of the field θ in the domains $\mathcal{M}_1, \mathcal{M}_2, \mathcal{M}_3$ so the values $\theta_1, \theta_2, \theta_3$ should be regarded as given constants in finding the pattern $\{J_i\}$.

For this problem the set of independent variables involves five values J_1, J_2, J_3, J_0, and θ_0, whereas, the number of equations is equal to six. However, these equations are linearly dependent. Indeed, summing equations (1.20) and taking into account (1.17), (1.18) we obtain

$$J_0 - J_0\frac{\theta_0}{\theta_c} = \sum_{i=1}^{3} \frac{\tilde{P}^m - \tilde{P}^B}{R_i}. \tag{1.21}$$

Equations (1.19), (1.21) coincide with each other if

$$\frac{\tilde{P}^B - \tilde{P}^{B'}}{R_0} = \sum_{i=1}^{3} \frac{\tilde{P}^m - \tilde{P}^B}{R_i}. \tag{1.22}$$

The latter equality is fulfilled because the values $\{\tilde{P}^i\}$ have been established by the initial distribution of transport agent flows $\{\tilde{J}_i\}$. Therefore the system of equations (1.17)–(1.20) admits a solution.

For the branching point B' the branch 0 plays the same role as branches $i = 1, 2, 3$ for the point B, in particular, the value θ_0 should be treated as a predetermined parameter. Replicating these speculations practically one–to–one with respect to the point B' and then, going towards the stem we show that the total system of equations governing the transport agent flow on the network

N as a whole admits the solution with $\{P^i\} = \{\tilde{P}^i\}$. Whence, it follows that variations in the transport agent flow J_i through a branch i of the last level is determined by the value of θ_i only which is equal to the mean value of the field θ over the corresponding domain $\mathcal{M}_i$. The latter is responsible for the local relationship between the fields θ and η.

The existence of the local relation between the fields θ and η in such a simple form is a surprise because this relationship does not contain directly information on the complex geometry of the hierarchical network involving a tremendous number of elements. This fact is actually the main result of the present Section.

Concerning real systems in nature the obtained results enable one to study their evolution and behavior from two different standpoints individually. One problem is the analysis of architectonics of real natural systems and the product transport flow as well as information flow in them. Another is connected with the individual properties and behavior of system elements. From the standpoint of a living system the adaptation transport network and its elements differ in purpose. The transport network forms required flow of products and information that is not directly controlled by system elements. The system elements responding to a local information adapt individually.

The existence of a large hierarchical systems in nature and their capability for adapting to changes in the environment points the fact that they are organized and function approximately ideally. Therefore, the general principles of hierarchical system functioning found in the present paper are likely to be useful in the analysis of their function disturbance and adaptation.

In nature, for example, in living tissue in order to reduce this effect of the nonideality arterial and venous beds contain a system of anastomoses, i.e. vessels joining arteries or veins of the same level. So, architectonics of large natural systems is organized in such a manner that their functioning has to be ideal as perfect as possible.

For different natural systems the variables θ and η are distinctive in meaning. For example, for living tissue the variable θ can be treated as the concentration of carbon dioxide, or the tissue temperature, the variable η is the blood flow rate, and the blood pressure plays the role of the external potential E_{ext} and $d = 3$. A similar situation takes place in respiratory systems, where the variable θ is the oxygen concentration. In economic systems the quantity η is the flow rate of goods and the variable θ is the price. In this case the external potential E_{ext} is likely to be treated as the total utility function of the production process in a certain industry. In models for organization and functioning of firms the basic medium is the firm bottom comprising workers, the variables η and θ are quantities proportional to the wages of workers and amount of products, respectively. Concerning ecological systems the variables η and θ seem may be regarded as the rate of a biomass flow and the energy stored up in a biomass unit.

1.4 On hierarchical structures arising spontaneously in markets with a perfect competition

In real economic systems there must be a certain mechanism that informs people what they should produce and in what amount, what work should be performed for this production etc. Broadly speaking, there are two essentially different mechanisms governing the economic life. One of them is based on the state hierarchical system, where the behavior of each economic agent is directly controlled by one of the higher rank [25]. According to another mechanism the correlation in people behavior is grounded on the spontaneous order which arises through information obtained by individuals in the interaction with their local economic circumstances. The latter mechanism is actually the core of real markets [25, 91, 11].

In the present Section we pay attention to the fact that the market can also contain hierarchical structures arising spontaneously where each of their elements responds to the corresponding piece of information, solves its individual problem, e.g. "maximize" its own profit, which, nevertheless, leads to the perfect functioning of the system as a whole. The ideality in the behavior of these systems is caused by self-processing of information at each hierarchy level, i.e. by a synergetic mechanism of self-regulation [60].

Let us, first, discuss the reason and the place where such hierarchical structures come into existence.

The existence of a tremendous amount of goods in market, in contrast to a relatively small number of raw materials as well as to the producer specialization shows that there must be a highly complex network which links different producers with one another, transforms raw materials and, finally, supplies consumers with the goods required. The structure of such a network is schematically illustrated in Fig. 1.7. A branch of the given network (e.g., branch i) joining the nearest nodes represents a collection of producing firms that can be regarded as identical from the standpoint of their input and output. The firms are linked with one another by sell-buying processes, the output of firms belonging to higher ranks being input for firms of lower ranks. The nodes specify these sell-buying interactions. Firms at the last level sell directly to ultimate consumers, supplying the latter with different types of goods. In other words, the input and output of different firms form in the given network a material flow $\{X_i\}$ going from raw material stems to the consumer medium.It should be noted that this sell-buying interaction singles out a certain economic system under consideration that, on one hand, involves a great number of participants and exhibits a general property typical for all markets, and, on the other hand, is a small part of the whole market society producing goods of a certain type. For example, steel, food, clothing industries may be regarded as such microeconomic markets. In living organisms, regional vascular network of different organs play the same role as microeconomic markets do in the human society. In these terms the material flow corresponds to the blood flow in vessels and the consumer medium

Figure 1.7: Schematic representation of the market network.

is related to the cellular tissue.

Particular interconnections between different firms can occur and disappear during formation and evolution of the market under consideration. These interactions are governed by trade with each other. The latter process stimulates the money flow within the market network in the direction opposite to the material flow, i.e. in the direction from the consumers to the producers of raw materials. The conservation of money at the nodes enables them to play a role of a certain aggregated information of the state of the consumer medium as well as of the firm activity. The matter is that for a certain collection of firms, e.g. firms, belonging to branch i, to be able to supply firms of the lower rank linked directly with the given firms of the network with the required input it is necessary and sufficient that these firms possess the information characterizing the consumer state in the region controlled by the given firms as a whole. Such information is directly reflected in the price of the output.

A change in the consumer demand leads to variations of the material flow within the market network. The latter, in turn, causes the firm's profits to vary and, thus, the firms to increase or decrease their activities. In particular, there are no barriers to the entry of new firms in respect to the short-run profits being made in the given market. When the competition is perfect this process will cause the average profit at each branch to be maintained at zero value [91, 11].

In the present Section within the framework of the market with a perfect competition we show that there may be certain hierarchical structures arising spontaneously which supply consumers with goods ideally. This means that

at the first approximation the change in demand at one point of the consumer medium does not cause variations in the goods flow at its other points although the material flow varies across all branches belonging to all the hierarchy levels.

Let us begin by setting up the model.

1.4.1 Model

Let us consider an industry structure in the market involving the consumer medium $\mathcal{M}$ and hierarchical network $\mathcal{N}$ of the tree form supplying it with goods (Fig. 1.8).

The material flow in the given network is determined by the collection $\{X_i\}$ of the total firm product X_i at branch i measured in mass units. Because of the conservation of materials at each nodes, e.g. node B, we may write the expression

$$(X_i)_{in} = \sum_{j_B} (X_j)_{\text{out}}, \tag{1.23}$$

where $(X_i)_{in}$ and $(X_j)_{\text{out}}$ are the total product at the branches going in and out of the node B and the sum runs over all the branches leaving this node. In other words , the output $(X_i)_{in}$ of firm i is equal to the sum of the inputs of the firms $(X_j)_{\text{out}}$.

The branch i is assumed to contain n_i individual firms treated as identical, at least, on the average. The total product X_i at the branch i is equal to the sum of the products x_i produced by these n_i firms, viz.:

$$X_i = n_i x_i. \tag{1.24}$$

Variations in the number of firms $\{n_i\}$ is the market response to change in the consumer demand. The output collection $\{X_i\}$ of the firms belonging to the last level of the network determines the corresponding set of goods flows $\{X_i^*\}$ through the consumer medium:

$$X_i = X_i^*.$$

For the sake of simplicity we suppose that the i-th consumer is supplied only by one of the firms at the last level. The latter can be justified, if the consumers are substantially distinguished by there location in physical or goods space.

The trade interaction at a node B gives rise to a price P_B for a mass unit of the material exchanged in this interaction. As a result, the money flow aggregated at branch i due to trade interaction is $X_i(P_i^{(s)} - P_i^{(b)})$, where $P_i^{(s)}$, $P_i^{(b)}$ correspond to the nodes $B_i^{(s)}$, $B_i^{(b)}$ at which firms i play the role of a seller and buyer, respectively (Fig. 1.8). The individual profit of a firm belonging to branches i is

$$\pi_i = x_i(P_i^{(s)} - P_i^{(b)}) - tc_i(x_i), \tag{1.25}$$

where the former term is its revenue and the latter one is its total cost given by the expression [91]

$$tc_i(x_i) = k_i + a_i x_i + b_i x_i^2. \tag{1.26}$$

The set of parameters $\{k_i, a_i, b_i\}$ is considered to be constants given beforehand. The total profit Π_i at branch i is

$$\Pi_i = X_i(P_i^{(s)} - P_i^{(b)}) - [k_i n_i + a_i X_i + \frac{1}{n_i} b_i X_i^2].$$

The individual purpose of each firm is to maximize its profit with respect to the product, which leads to the expression

$$\frac{\partial \pi_i}{\partial x_i} = 0, \tag{1.27}$$

whence it follows that

$$P_i^{(s)} - P_i^{(b)} = a_i + 2b_i x_i. \tag{1.28}$$

At the final stage firms sell their goods to ultimate consumers; accordingly, the price $P_i^{(s)}$ is determined by the consumer market demand. Assuming that at this final stage $P_i^{(s)} = d_i^* - f_i^* X_i^*$, where d_i^*, f_i^* are supposed to be predetermined constants and the firms transform each unit of their input into one unit of the output after a processing cost of c_i^* per unit is incurred [91] we obtain.

$$\Pi_i^*(X_i^*) = X_i^*(d_i^* - f_i^* X_i^*) - P_i^{(b)} X_i^* - c_i^* X_i^* \tag{1.29}$$

The condition of the profit $\Pi_i^*(X_i^*)$ attaining maximum with respect to X_i^* leads to the expression

$$P_i^{(b)} = d_i^* - c_i^* - 2f_i^* X_i^* \tag{1.30}$$

Perfect competition in the market maintains the profit $\pi_i(x_i)$ at the zero value [11], thus, for each firm of branch i of the network it can be written

$$\pi_i(x_i\,|P_B\,)| = 0 \tag{1.31}$$

for the $\{x_i\}$ and $\{P_B\}$ related to each other by expressions (1.28), (1.30).

Expression (1.28), (1.30) together with the conservation (1.23) of products at the nodes establishes such prices at the nodes that meet the maximum profit condition for all the firms and satisfy the market equilibrium.

Now let us analyse the characteristic properties of the stated model.

1.4.2 Perfect self-regulation

Substituting (1.28) into (1.31) we find that

$$P_i^{(s)} - P_i^{(b)} = a_i + 2\sqrt{k_i b_i} \tag{1.32}$$

Figure 1.8: Industry structure of the tree form.

This result shows that the difference $P_i^{(s)} - P_i^{(b)}$ for each branch i is actually determined by the internal parameters of the technology, production efficiency, and the market rate of the capital rather then, by the consumer demand. The latter follows directly from a perfect competition. This property enables us to find the price at a given node. Setting for the sake of simplicity for firms belonging to the stem the buyer price equal to zero (or ignoring it) we get for a node B

$$P_B = \sum_{i \in \mathcal{P}_B} \left(a_i + 2\sqrt{k_i b_i} \right) \tag{1.33}$$

where $\mathcal{P}_B$ is a path on the network connecting the given node B with the stem.

Returning to the initial network shown in Fig.1.7, we can replicate the same speculations regarding with respect to the material flow distribution $\{X_i\}$. In this way we will again obtain formula (1.33) where, however, the path $\mathcal{P}_B$ is not unique. Therefore, except for the degenerate cases, under a perfect competition the firms that belong to the paths (fine lines on Fig. 1.7) with larger values of P_B have to leave the market. The latter will convert the initial production network of a complex geometry into a hierarchical network of the tree form (solid line in Fig. 1.7) which minimizes the price.

According to (1.30) and (1.33) the goods flow X_i^* demanded by consumer i can be given as

$$X_i^* = \frac{1}{2f_i^*}[d_i^* - c_i^* - \sum_{j \in \mathcal{P}_i} (a_j + 2\sqrt{k_j b_j})] \tag{1.34}$$

where $\mathcal{P}_i$ is the path leading from the stem to the given point i of the consumer medium. The state of the consumer medium is entirely specified by the set of parameters $\{d_i^*, f_i^*\}$. Thus, the change in the consumer demand reflects in time variations of the parameters $\{d_i^*, f_i^*\}$. Assuming the technological parameters $\{a_i, k_i, b_i, c_i^*\}$ of the production to be constant it can be seen from (1.34) that the goods flow X_i^* through any given point i of the medium $\mathcal{M}$ is controlled solely by its own parameters $\{d_i^*, f_i^*\}$. Time variations of the parameters $\{d_i^*, f_i^*\}$ at other points do not affect the goods flow at the given point i. This property can be naturally treated as perfect self-regulation.

Conservation of materials at the nodes (1.23) allow us to find the material flow X_i going through a given branch i as a function of the goods flow through the consumer medium. Specifically,

$$X_i = \sum_{j \in \mathcal{M}_i} X_j^* \tag{1.35}$$

where $\mathcal{M}_i$ is the consumer medium region where the goods flow as a whole is directly controlled by the given branch (Fig. 1.8). In particular, expressions (1.28), (1.32), (1.35) yields the number n_i of independent firms participating in the production of the output X_i:

$$n_i = \sqrt{\frac{b_i}{k_i}} \sum_{j \in \mathcal{M}_i} \frac{1}{2 f_j^*} \left\{ d_j^* - c_j^* - \sum_{j' \in \mathcal{P}_j} (a_{j'} + 2\sqrt{k_{j'} b_{j'}}) \right\} \tag{1.36}$$

The last expression reflects the ability of the market as a whole to respond to changes in the consumer demand by an appropriate change in the number of firms n_i.

An opinion exists that the market economies are based solely on spontaneous trade interactions between buyers and sellers in contrast to the centrally-planned economies which are organized hierarchically. In the present Section we tried to show that "free markets" might also contain complex hierarchical structures, which, at first, arise spontaneously, and then, minimize efforts to satisfy the consumer demands. Such hierarchical systems are likely to provide the unique feasibility of self-processing of information on which products to be supplied, how much each of them to be produced, and in what ways to distribute them. Different aspects of this problem has been considered also in works [33, 34, 35, 71].

Real markets are not, naturally, perfect, firms are not identical and etc. This leads to violation of the market ideal self-regulation. Nevertheless, we think the presented model may be useful in analyzing real processes in market if used as the first approximation since it enables one to take directly into account possible complex interactions between producers.

Figure 1.9: Linear trophic chain (solid lines) and an additional chain (a thin line) joined at the point B.

1.5 Self–regulation of trophic flows on hierarchical networks

Let us consider some problems in interaction of different species forming a certain closed ecological system. One of the classic approaches to the dynamics of such systems is the Lotka–Volterra model. This model characterizes a given species i by the number n_i of its members measured in biomass units and treated the species interaction in terms of feeding relationships where one species plays the role of predators or preys with respect to another. In other words, time variations in the values $\{n_i\}$ of the given ecosystem involving N species are governed by the collection of equations

$$\frac{\partial n_i}{\partial t} = n_i \left(k_i(n_i) + \sum_{j=1, j\neq i}^{N} a_{ij} n_j \right) \tag{1.37}$$

where $k_i(n_i)$ is the intrinsic growth parameter of the species i depending generally on n_i, the quantity a_{ij} is the constant of the trophic interaction between the species i, j which takes a positive or negative value providing the species i plays the predator or prey role in the ij–interaction, and the matrix (a_{ij}) is antisymmetric that is $a_{ij} = -a_{ji}$ for $i \neq j$ and $a_{ii} = 0$.

The architectonics of the ecological system determines the matrix (a_{ij}), and a linear trophic chain (1.9) of $2N$ elements is one of the widely studied

models for which the constants $\{a_{ij}\}$ are different from zero for the nearest neighbors only and $a_{i(i-1)} > 0$. Let us consider the steady state solution of the system of equations (1.37) assuming for the sake of simplicity $k_1 = \alpha$, $k_{2N} = -\beta$, and $k_i = 0$ (for $i = 2, 3, ..., 2N - 1$), where α and β are certain positive constants. Omitting trivial mathematical manipulations we get for the even terms $i = 2, 4, ..., 2N$

$$n_2 = \frac{\alpha}{a_{21}}, \quad n_i = \frac{a_{(i-1)(i-2)}}{a_{i(i-1)}} n_{i-2} \tag{1.38}$$

and for odd ones $i = 2N - 1, 2N - 3, ..., 1$

$$n_{2N-1} = \frac{\beta}{a_{2N(2N-1)}}, \quad n_i = \frac{a_{(i+2)(i+1)}}{a_{(i+1)i}} n_{i+2}. \tag{1.39}$$

Whence, it follows that the population n_i of the even species is actually directly determined by the generation rate α of the initial food source, whereas that of the odd species is controlled by the life time of the last predators. The higher the generation rate, the greater the total population of the ecosystem which reflects the fact of its adaptation to variations in the environment. In particular, the population n_{2N} of the last species also increases as the generation rate α grows.

If there is another trophic chain connected with the former one at the point B then, the two chains may be considered independently of each other, since, at the point B partial biomass flows J, J' are controlled by the interaction of the last and the last but one elements individually for each chain. So, in the general case such trophic chains have to come into conflict with each other causing one of them to vanish under stationary conditions. Indeed, otherwise according to (1.38) the population n_{2N} of the last species would be determined by the different biomass flows J, J' at the same time. In other words, for example, an increase in the generation rate α of the initial food for the former chain will increase the population of the last level predators, which in their turn will lead to local growth of the flow J' causing finally the latter chain to vanish as a whole. As a rule, such a behavior of interacting trophic chains is also the case in the dynamics when their populations vary in time (1.37).

However, the existence of a huge amount of species in nature and the growth of their variety as one goes from higher to lower organisms show that there must be a certain mechanism which, in principle, can stabilize ecosystems and enable them to form hierarchically organized structures.

In the present Section we discuss a possible mechanism for trophic networks of the tree form that prevents from preys being killed by the predators whose population increases because of the growth of a biomass flow in the neighboring branch of the trophic network.

First, we consider biomass flows on the trophic tree shown in Fig. 1.10 whose distribution is controlled by the classic Lotka–Volterra model with the coefficients $k_i = 0$ for all the species except the species of the last level feeding on the basic medium M of initial food and the predators forming the tree stem. For the former and latter we set $k_i = \alpha_i$ and $k_{\text{stem}} = -\beta$, where $\{\alpha_i\}$ and β

Figure 1.10: Hierarchically organized irregular trophic network.

are certain positive constants. Going along the trophic tree from the medium M to the stem we meet alternately species whose population is actually directly determined by the state $\{\alpha_i\}$ of the medium M and species whose population may be treated as a free variable until we reach the stem or a branching point. In Fig. 1.10 the former and the latter are labelled by the symbols "m" and "s", respectively. In mathematical terms the movement from the species of the last level to the stem and in the opposite direction is associated with solving the set of equations (1.9) by the successive iteration. The main problem of this procedure occurs when we meet a node where, as it has been shown for linear chains, the equations can be incompatible. There are three types of nodes represented in Fig. 1.10 by the branching points A, B, and C. Let us analyse their properties individually.

The simplest situation is realized at the point A, where the branches entering this point are actually independent of each other, the branch, going out of the point A, is of the "s" type, and the corresponding species have a net food source of the fixed rate of biomass generation $\alpha_s = a_{s,m_1}n_{m_1} + a_{s,m_2}n_{m_2}$ formed by the species m_1, m_2. Passing such a node we cannot meet any problem in iterating equations (1.37) until we reach another node.

At the point B iterating equations (1.37) is also associated with no difficulty. The steady state conditions for the preys "s_1" interacting with the predators at the point B determine the population of these predators "m_1" which, therefore, must be regarded as species of the "m" type. The value n_{m_1} determines the population n_{s_2} of the species "s_2". The population n_{s_1} of the species "s_1" is a free variable which is will be found by the following iterations.

Dealing with the point C we meet the main problem. Going along different

Figure 1.11: The node connecting one type of predator with two types of prays.

branches "s_1" and "s_2" and entering this node we have to ascribe two different values of the population n_m to the same species "m" what is impossible in the general case and so, one of the branches "s_1", "s_2" will be wiped out.

In order to avoid such a trouble we proposed the following self–regulation model. Let us, first, single out one branching point on the trophic tree and consider the interaction between its elements (1.11). According to

(1.37) the interaction between the predators i and the preys i_1, i_2 gives rise to the partial biomass flows J_1, J_2 going through the point C determined by the expressions

$$J_1 = a_1 n n_1, \quad J_2 = a_2 n n_2, \tag{1.40}$$

where n, n_1, n_2 are the populations of the predators and the corresponding preys. The total biomass flow J entering the species of the predators during their chase is

$$J = J_1 + J_2 = (a_1 n_1 + a_2 n_2) n. \tag{1.41}$$

In the classic Lotka–Volterra model the interaction coefficients a_1, a_2 are treated as given constants. In the model we consider the predators to be "active"; they can change the strategy of chase in order to maximize the total biomass flow J. In mathematical terms this means that the interaction coefficients $a_1(\phi)$, $a_2(\phi)$ are certain functions of the chase strategy ϕ (treated as an additional free variable belonging to the interval $[0, 1]$), and that the predators "choose" the chase strategy in such a way that the function $J(n, n_1, n_2, \phi)$ attains its maximum for fixed values of n, n_1, n_2, that is

$$J = n \max_{\phi \in [0,1]} \left[a_1(\phi) n_1 + a_2(\phi) n_2 \right]. \tag{1.42}$$

The maxima of the functions $a_1(\phi)$, $a_2(\phi)$ are attained at different values $\phi_1 = 0$ and $\phi_2 = 1$ of the variable ϕ which means that the chase specialization with respect to one preys reduces the chase efficiency with the other preys. The general form of the function $a_j(\phi, \phi_j)$ is demonstrated in Fig. 1.12.

Condition (1.42) imposed on the chase strategy leads to the dependence $\phi = \phi(n_1, n_2)$ which in turn gives rise to the dependence of the interaction

Figure 1.12: Schematic view of functions $a_1(\phi, \phi_1), a_2(\phi, \phi_2)$.

coefficients on the prey populations, $a_1 = a_1(n_1, n_2)$, $a_2 = a_2(n_1, n_2)$. Thus, a decrease in the population of one preys or an increase in the others will reduce the chase efficiency with respect to the former preys, preventing them from disappearing. This is actually the essence of the given self–regulation model.

In order to illustrate this effect we consider in detail the case when the functions $a_1(\phi, \phi_1)$, $a_2(\phi, \phi_2)$ are of the form

$$a_1(\phi, \phi_1) = a_1^0 \left[1 - \phi^2\right], \quad a_2(\phi, \phi_2) = a_2^0 \left[1 - (1 - \phi)^2\right], \tag{1.43}$$

where the parameters a_1^0, a_2^0 are constant. The asymptotic behavior of the functions $a_1(\phi) \to 0$ as $\phi \to \phi_2 = 1$ and $a_2(\phi) \to 0$ as $\phi \to \phi_1 = 0$ allows us to treat such a regulation as ideal because under these conditions none of the species can be wiped out. Substituting (1.43) into (1.42) and maximizing the result we find

$$\phi(n_1, n_2) = \frac{a_2^0 n_2}{a_1^0 n_1 + a_2^0 n_2} \tag{1.44}$$

and

$$a_1(n_1, n_2) = a_1^0 \frac{a_1^0 n_1 (a_1^0 n_1 + 2a_2^0 n_2)}{(a_1^0 n_1 + a_2^0 n_2)^2}, \quad a_2(n_1, n_2) = a_2^0 \frac{a_2^0 n_2 (2a_1^0 n_1 + a_2^0 n_2)}{(a_1^0 n_1 + a_2^0 n_2)^2}. \tag{1.45}$$

As it must $a_1(n_1, n_2) \to 0$ as $n_1 \to 0$ and $a_2(n_1, n_2) \to 0$ as $n_2 \to 0$.

In order to demonstrate this model we will show for the point C in Fig. 1.10 that from the standpoint of species "m" the branches "s_1" and "s_2" may be aggregated into one branch connected with an effective feeding medium. Let n, n_1, and n_2 be the populations of species "m", "s_1", and "s_2". Then, the conservation of a biomass in species "s_1", "s_2" gives the equations

$$a_1(n_1, n_2) n = \alpha_1, \quad a_2(n_1, n_2) n = \alpha_2. \tag{1.46}$$

For their compatibility it is required that

$$\frac{a_1(n_1, n_2)}{a_2(n_1, n_2)} = \frac{\alpha_1}{\alpha_2}. \tag{1.47}$$

Substituting (1.45) into (1.47) and solving the obtained equation we find that the total biomass flow through the species "m" is equal to

$$J = a_{\text{eff}} n C = \alpha_{\text{eff}} C, \tag{1.48}$$

where $C = n_1 + n_2$ is the total population of preys being in contact with the predators "m" and the effective coefficients

$$a_{\text{eff}} = \frac{\rho^2 + \rho + 1}{\rho + 1} \frac{a_1^0 a_2^0}{a_1^0 + \rho a_2^0}, \tag{1.49}$$

$$\alpha_{\text{eff}} = \frac{\alpha_2 a_1^0 + \rho \alpha_1 a_1^0}{a_1^0 + \rho a_2^0}. \tag{1.50}$$

and the constant

$$\rho = \left(\frac{\alpha_1 a_2^0}{\alpha_2 a_1^0} - 1 \right) + \sqrt{\left(\frac{\alpha_1 a_2^0}{\alpha_2 a_1^0} - 1 \right)^2 + \frac{\alpha_1 a_2^0}{\alpha_2 a_1^0}}.$$

Expression (1.48) allows us to regard the given fragment of the trophic tree as a linear chain.

Concluding the present Section we would like to note that such an "active" trophic network can adapt to variations in the environments without any dramatic reorganization. The behavior of real ecological systems is certain to be much more complicated, nevertheless, it is likely that active behavior of species not, only predators but also preys lead to extension of a species variety in nature (see also [33, 37]).

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